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THE ORIGIN OF THE HEART ENDOTHELIUM IN AMPHIBIA.¹

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The origin of the heart endothelium in Amphibia has been the subject of several special investigations and of a considerable volume of discussion. The question of fact may now be regarded as settled. The work of Brachet has given definite and conclusive evidence that the endothelium is derived directly from the entoblast, as had been shown to be very probable by the earlier work of Rabl and Schwink. The question now of interest is, how is the derivation of the heart endothelium from the entoblast in amphibia to be harmonized with its known origin from the mesoblast in all other vertebrates? The problem is that of the homology of the heart endothelium of amphibia. Granted that, as Ziegler contends, the condition in amphibia is to be regarded as the result of cœnogenetic modification, exactly what is the modification that has taken place? What is the definite explanation of the striking difference between amphibia and other vertebrates? As Brachet has pointed out, the term "cœnogenesis" can not be invoked as a magic symbol to dispense with the whole matter. It is not enough to say that in amphibia the endothelial cells remain connected with the entoblast until a late period and become separated after the mesoblast sheet has split off. This offers no escape from the difficulty pointed out by Morgan ('97, p. 151) that the heart endothelium must be considered to have a different origin from the rest of the heart.

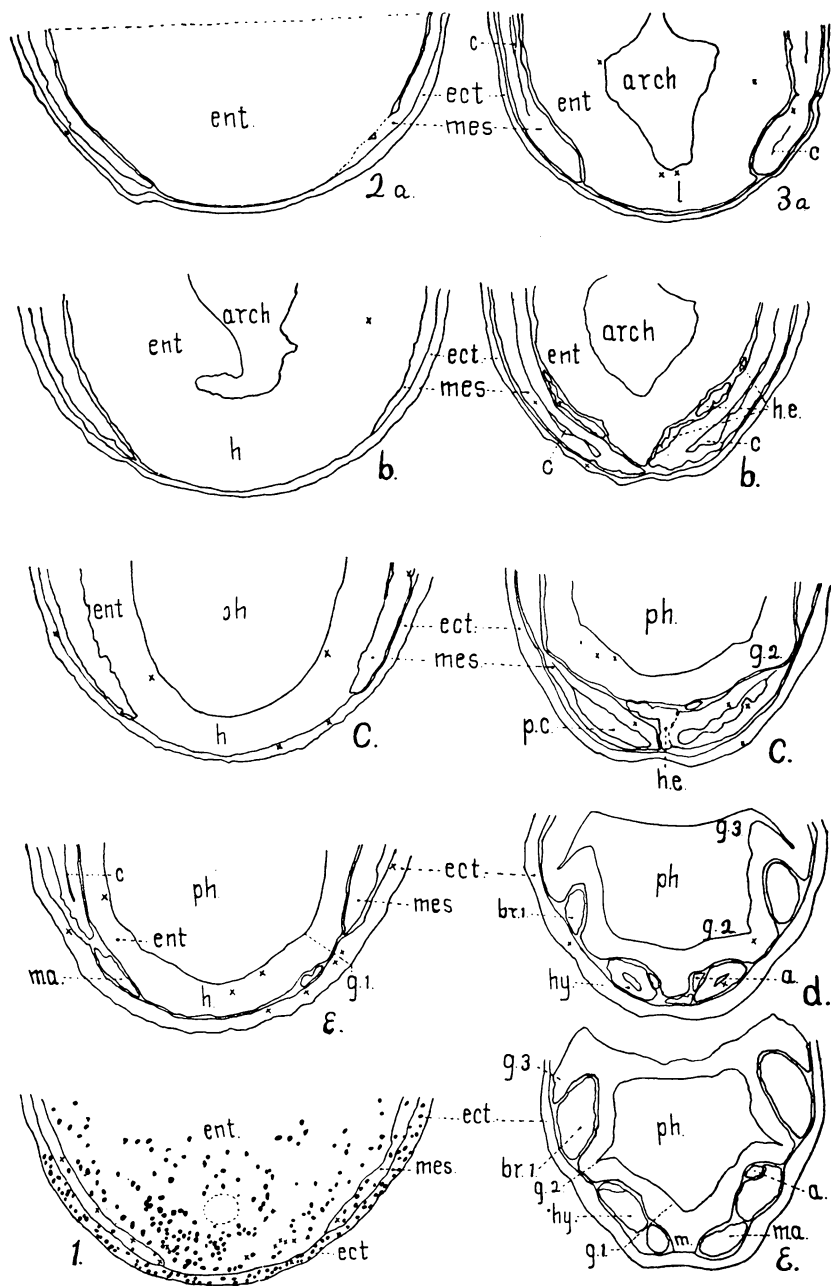
The work upon which the present paper is based has been done upon the eggs of a salamander which have been used for class study for the past two years. The species has not been identified because no adults have yet been taken. I hope at some later time to give a description of these eggs and to deal with some other features of the embryology of the species. The eggs

¹Studies from the Zoölogical Laboratory of West Virginia University, No. 7 February 27, 1903.

have proved very favorable for study and the facts are so clearly made out that they are thought to offer a solution of the problem.

The earliest indication of the formation of the heart endothelium is found in the rapid multiplication of the cells of the entoblast just behind the mouth anlage, at a period when the head is slightly turned downward and before the gill slits have begun to appear. As shown in Fig. 1, the nuclei in this part of the entoblast are small, rounded, very numerous and closely crowded, and many of them are in some stage of mitosis. The nuclei in the remainder of the entoblast are larger and irregular, being much distorted by pressure of the yolk grains, and mitotic figures are rare. The area described extends for a considerable distance backward from the mouth, and the same conditions prevail on the cephalic surface and the sides of the pharynx close to the mouth anlage. Rapid growth in these latter regions continues later than behind the mouth and is connected with the formation of head mesenchyme. The region of growth behind the mouth is noticeable in both transverse and sagittal sections, but it is of short duration and in slightly later stages the cells are relatively larger and the nuclei have the appearance of resting nuclei. At the point nearest the mouth the cell divisions continue until the time of separation of the heart endothelium.

The formation of the mesoblast and its early differentiation furnish the facts of greatest significance for our problem. In the head and anterior part of the trunk the mesoblast is split off from the entoblast to a point some distance from the mid-ventral line, where the delamination appears to stop. That this is a definite limit beyond which delamination does not go is evidenced by the distinct separation between entoblast and mesoblast which often occurs even in very early stages (Fig. 2, *a* and *b*), by the total absence of nuclei in the outer half of the entoblast ventral to the limit mentioned, and by the future history of the ventral portion of the mesoblast. Mitotic figures often appear very early in the ventral edge of the mesoblast sheet (Fig. 1), and although they do not appear in the sections drawn in Fig. 2, they are usually more numerous there than elsewhere in the mesoblast. The result of rapid growth here is to cause a decided thickening of the ventral edge of the mesoblast, and in this thickening the body



FIGS. 1, 2 AND 3.

cavity early makes its appearance (Fig. 3, *a*). With further growth the body cavity enlarges and the entoblast is laterally compressed between the cavities of the two sides. As a result, the growing entoblast behind the mouth, above described, takes on the form of a keel. Later the body cavity (pericardial cavity) spreads ventrally and mesially, and the mesoblast insinuates itself between the heart endothelial cells and the ectoblast and later between these cells and the entoblast. This movement is due entirely to the growth and spreading of the mesoblast earlier split off and not to a further delamination from the entoblast. There is no sign of any further delamination of mesoblast after the stage shown in Fig. 2, but on the contrary the mesoblast grows continually more and more sharply distinct from the entoblast after that period. The pushing down of the mesoblast in the region of the heart, which accompanies the enlargement of the pericardial cavities, is well advanced while the thickened ventral edge of the mesoblast farther caudally has not shifted its position (Fig. 3, *a*, *b*, *c*). The region in which the delamination of mesoblast does not reach the mid-ventral line extends caudally to a point a little behind the middle of the embryo and this region probably includes the blood island described by Brachet. The writer has not yet fully investigated this region, but if the surmise here made is correct, the reasoning applied to the question of the heart endothelium will apply equally well to the blood island. To recapitulate, there is a mid-ventral area or keel of entoblast extending backward from the mouth anlage, from which no mesoblast is split off in the species studied. From this area the heart endothelium (and perhaps the blood) are formed.

A second fact of some interest for us is that the mesoblast shows a tendency to split off late, so that it is already divided into regions when it first separates from the entoblast. This is seen especially in the formation of the mandibular arch. As shown by Fig. 2, *e*, the mandibular arch mesoblast, at its first appearance is separated from the rest of the mesoblast by the first gill slit, and it never has any connection with the mesoblast bounding the pericardial cavity. Indications of the second gill slit also appear very early, so that in some cases the hyoid arch, which is continuous with the pericardial cavity, seems to be split

off from the entoblast separately from the rest of the mesoblast. Finally, single cells wander off from the cephalic surface of the entoblast and go immediately to the formation of head mesenchyme.

The mode of formation of the heart endothelium from the ventral keel of entoblast differs in details in different forms. In the Urodeles studied by Brachet, the keel of entoblast extending from the mouth anlage to the region of the liver splits off as a continuous rod, the cells of which later arrange themselves into a tube. In the species studied by the writer the cells of this keel do not remain in a continuous rod but split off singly or in groups of a few cells and form a loose mass which remains connected with the entoblast longest at the end nearest the mouth. At this point there is continued growth and there is probably a migra-

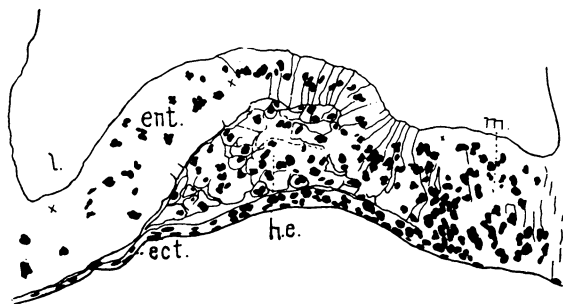


FIG. 4.

tion of cells from this point backward, and also upward into the several branchial arches, to form the aortic arches. The splitting off of this keel of entoblast is taking place simultaneously with the spreading ventrally and mesially of the pericardial mesoblast. My preparations leave no doubt whatever that the heart endothelium is formed from the most superficial portion of the entoblast in the mid-ventral region and that the lateral sheets of mesoblast are formed wholly outside of this area. Brachet's description makes it clear that the same thing is true of the Urodeles which he studied, but this important relation seems not to have attracted his attention and the fact is not mentioned by him.

We are now able to state definitely the nature of the cœnogenetic modifications connected with the formation of the heart endothelium in amphibia. According to the earlier accounts

which have recognized the derivation of the endothelium directly from the entoblast, the mesoblast sheets were split off first, and later — consequently from deeper layers of entoblast — the cells destined to form the heart endothelium were split off. Since in other vertebrates only one layer of cells is split off and the heart endothelium is differentiated from a part of this mesoblast, the conclusion that the endothelium of amphibia has a different origin from that of other vertebrates was unanswerable. In the species studied by the writer (and also, apparently, in those described by Brachet) the mesoblast sheets are split off earlier from the entoblast except in the region in which the heart endothelium will appear, and later the endothelium is split off from a part of the entoblast which has not given rise to any (other) mesoblast. Therefore, in these forms, the heart endothelium is derived from the same source as the mesoblast sheets, namely from the superficial layer of entoblast, and the difference between these amphibia and other classes of vertebrates consists only in a somewhat general tendency for the mesoblast to split off relatively late and to be marked out into definite organs, or organ-anlagen, at the moment of splitting off. This is seen not only in the splitting off of the heart endothelium at a little later time and separately from the rest of the mesoblast, but also in the same mode of formation of the mandibular and hyoid arches and of a part of the head mesenchyme. The writer believes that a reëxamination of other amphibia, at least of Urodeles, at the proper stages of development will show the process here described to be characteristic for amphibia. In brief, then, the heart endothelium of amphibia is strictly mesoblastic, although it is not at any stage identified with the undifferentiated mesoblast, being split off from the entoblast in the same manner as the rest of the mesoblast, but somewhat later and separately.

DESCRIPTION OF FIGURES. ABBREVIATIONS.

a., aortic arch cells; *arch.*, archenteron; *br. 1*, first branchial arch; *c.*, coelome; *ect.*, ectoblast; *ent.*, entoblast; *g. 1*, *g. 2*, *g. 3*, first, second, and third gill slits; *h.*, heart region; *h.e.*, heart endothelium; *hy.*, hyoid arch; *l.*, liver region; *m.*, site of mouth; *m.a.*, mandibular arch; *mes.*, mesoblast; *p.c.*, pericardial cavity; *ph.*, pharynx. Small crosses indicate the position of mitotic figures. In Figs. 1 and 4 resting nuclei are shown as black spots.

FIG. 1. Transverse section through the ventral part of a young embryo immediately behind the site of the mouth, to show the area of growth in the entoblast preparatory to the formation of the heart endothelium. The dotted circle indicates the position in which the foregut appears in the next section forward.

FIG. 2, *a, b, c, e*. Transverse sections nos. 212, 224, 235, 251 of an embryo in which the first gill slit has just made its appearance. Sections 10 microns thick.

FIG. 3, *a, b, c, d, e*. Transverse sections nos. 273, 292, 306, 318, 325 of a later embryo in which the separation of the endothelial cells from the entoblast is nearly completed. Sections 10 microns thick. The sections shown in Fig. 3, *a, b, c, e* are approximately at the same levels as those shown in Fig. 2, *a, b, c, e*, respectively.

FIG. 4. Median sagittal section of the region between the mouth and liver of an embryo of the same age as that shown in Fig. 3. Cell boundaries are shown wherever they can be seen. The heart endothelial cells are evidently continuous with the entoblast behind the mouth, but independent at all other points.

All figures were drawn with Zeiss apochromatic lenses and camera. Figures 1, 2, and 3 were drawn with 16 mm. objective and no. 4 ocular; Fig. 4 with 8 mm. objective and no. 4 ocular, and all have been reduced to one third in reproducing.

BIBLIOGRAPHY.

Brachet.

- '98 Developpement du coeur chez les Amphibiens urodeles. Archives d'Anatomie micr., T. 2, p. 251-304, 1896.

Morgan.

- '97 The Development of the Frog's Egg, an Introduction to Experimental Embryology. New York, 1897.

Ralb.

- '86 Ueber die Bildung des Herzens der Amphibien. Morph. Jahrb., Bd. 12, pp. 252-273. 1886.

Schwink.

- '91 Untersuchungen über die Entwicklung des Endothels und der Blutkörperchen der Amphibien. Morph. Jahrb., Bd. 17, pp. 288-333. 1891.

Ziegler.

- '02 Lehrbuch der vergleichenden Entwicklungsgeschichte der niederen Wirbeltiere. Jena, 1902.